

A NEW AMERICAN FAIRY SHRIMP,  
*LINDERIELLA SANTAROSAE*  
(CRUSTACEA: ANOSTRACA: LINDERIELLIDAE),  
FROM VERNAL POOLS OF CALIFORNIA, U.S.A.

Alain Thiéry and Michael Fugate

*Abstract.*—A new species of fairy shrimp, *Linderiella santarosae* (Anostraca: Linderiellidae), is described from vernal pools on the Santa Rosa Plateau Reserve, Riverside Co., California, U.S.A. The form of the basal outgrowth on antenna 2 of males and the spines on the resting eggs are the primary characters which distinguish *L. santarosae* from the other *Linderiella* species of western North America, northwestern Africa and southwestern Europe. *Linderiella santarosae* is also distinguished from *L. occidentalis*, the other Californian species, by fixed differences at two electrophoretic loci (PGM and PEP-D). The distribution of the five known species, each locally endemic to Mediterranean climatic regions, may be linked to a wider distribution of the genus in the past across the Laurasian continent.

Brtek (1964) erected the family Linderiellidae and the genus *Linderiella* based on an enigmatic anostracan (*Linderiella occidentalis* Dodds, 1923) from a lake (Lagunita) on the Stanford University Campus in Palo Alto, Santa Clara Co., California, U.S.A. Dodds (1923) originally placed *L. occidentalis* in the genus *Branchinecta*, and Linder (1941), in his review of the Anostraca, transferred it to the family Chirocephalidae and the genus *Pristicephalus*. Brtek (1964) separated *L. occidentalis* from the Chirocephalidae based on differences in the male reproductive structures.

The genus *Linderiella* is currently restricted to regions with a Mediterranean climate in the Northern Hemisphere. Species are found in Morocco (*Linderiella africana* Thiéry, 1986), France (*Linderiella massaliensis* Thiéry & Champeau, 1988), Spain (Alonso 1985) and California, U.S.A. (*L. occidentalis* Dodds, 1923). The genus inhabits pools and ponds with low mineralization that fill after winter rains (Alonso 1985, Thiéry & Champeau 1988, Eng et al. 1990).

During fieldwork in California from 1988 to 1991, one of us (MF) collected two species of anostracans from several vernal ponds and pools within the Nature Conservancy Reserve on the Santa Rosa Plateau, Riverside Co., California. One of the species was *Branchinecta lynchi* Eng et al., 1990, and the other was the new species in the genus *Linderiella* described in this paper.

#### Methods

Specimens were fixed in 10% formalin and preserved in 70% ethanol. Antennae, thoracic appendages and penes to be illustrated were removed under a WILD M7 stereomicroscope and observed with a WILD M20 compound microscope, both equipped with camera lucida. Measurements are given to the nearest 0.1 mm for the adults and to the nearest 2 mm for the diameter of the resting eggs. Total length includes the distal setae of the cercopods. Specimens observed on the scanning electron microscope (SEM) were dehydrated through a graded ethanol series to absolute ethanol, critical-point



Fig. 1. California collection sites for populations of *Lindieriella* used in this study. Open star indicates the type locality of *Lindieriella santarosae*, n. sp.; solid star, the type locality of *Lindieriella occidentalis* (Palo Alto); solid circle, Fields Rd. and Tim Bell Rd.; solid square, Prairie City OHV; open circle, sites sampled by Eng et al. (1990), open triangles, DB. 430 population and solid triangle, Marin Co. (DB. 878).

dried and coated with gold-palladium for observation in a Cambridge Stereoscan 360. Specimens of related species used for morphological comparisons are from the personal collections of A. Thiéry (*L. africana*: Daya Azigza, 6 Mar 1985, Middle Atlas, Morocco and *L. massaliensis*: pond of Saint Maximin, 7 Feb 1988, France) and D. Belk (*L. occidentalis*: California, DB, 430). Ad-

ditional specimens of *L. occidentalis* either were collected in the field or lab-reared from dry mud (see locations on Fig. 1): Lagunita, Stanford University, Palo Alto, type locality of *L. occidentalis* (soil sample collected Nov 1989, C. Sassaman): 4 ♂, length, 8.8–10.9 mm, 3 ♀ (1 ovigerous), length, 9.5–10.0 mm; Tim Bell Road (12 Mar 1988, coll. S. Morey): 5 ♂, length, 9.7–11.2 mm, 4 ♀ (2 ovigerous), length, 11.0–13.3 mm; Fields Road (12 Mar 1988, coll. S. Morey): 7 ♂, length, 9.7–10.6 mm; 7 ♀ (5 ovigerous), length, 9.6–12.0 mm; Prairie City OHV. (2 Feb 1990 coll. M. Fugate): 21 ♂, length, 10.0–13.2 mm, 25 ♀ (20 ovigerous), length, 12.6–18.0 mm, and Tehama Co. DB. 430 (28 Mar 1982): 8 ♂, length, 10.1–12.4 mm, 9 ♀ (9 ovigerous), length, 10.2–14.6 mm.

Allele frequencies were determined using starch gel electrophoresis (see Fugate 1992 for detailed methods) for three populations (Fields Road, 14 individuals; Tim Bell Road, 6 individuals; Lagunita, 10 individuals) of *Lindieriella occidentalis*, one population (Mesa de Burro, 14 individuals) of *Lindieriella santarosae* and one population of (7 individuals from Connecticut Valley Biological Supply) *Eubbranchipus vernalis* (Verrill, 1869) at the following eight loci: malic enzyme (ME), phosphoglucumutase (PGM), glucose-6-phosphate isomerase (PGI), phenylalanyl-proline peptidase (PEP-D), leucyl-alanine peptidase (PEP-C), Glucose-6-phosphate dehydrogenase (G6PD), isocitrate dehydrogenase (IDH), and aspartate aminotransferase (AAT). Nei's pairwise genetic distances ( $D$ ) were calculated from the allele frequency data and clustered with the UPGMA method using PHYLIP 3.4 (Felsenstein 1989). Nei's genetic distance ( $D$ ) is an estimate of the number of allelic substitutions per locus between two populations (Nei 1987 chap. 9).

*Lindieriella santarosae*, new species  
Figs. 2–10

*Material examined.*—Holotype ♂, USNM 266798, allotype ♀, USNM 266797 and 20

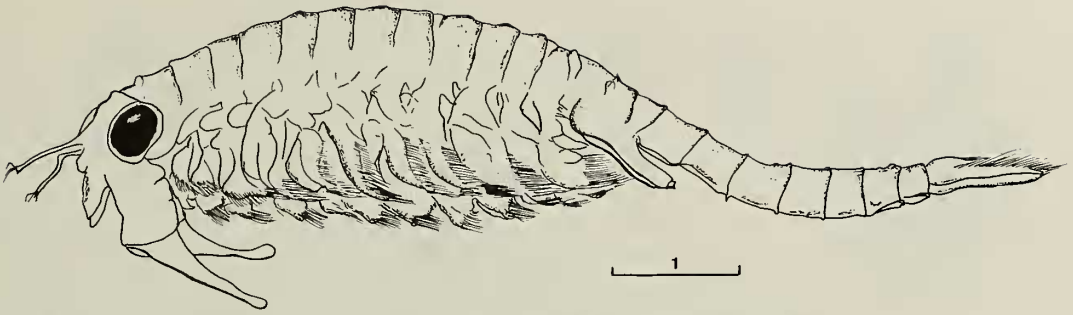


Fig. 2. *Linderiella santarosae*, n. sp.: habitus male, left lateral view (scale in mm).

paratypes, USNM 266796, Mesa de Burro; 18 paratypes, USNM 266795, Mesa de Colorado; 4 paratypes, Mesa de Colorado, Museum National d'Histoire Naturelle, Paris (MNHN Bp. 549). Additional specimens, fixed 1 August 1989 from Mesa de Colorado, also were used for the description. These individuals were lab-reared from soil samples collected 3 May 1988.

*Type locality.*—Vernal pools on the Santa Rosa Plateau Reserve, Riverside Co., California (Fig. 1). The reserve, located 6.5 km southwest of Interstate 15 on Clinton Keith Road (33°32'N, 117°17'W), is bordered on the northwest by the Santa Ana Mountains and on the east by agricultural and urban development surrounding the cities of Murrieta and Temecula.

*Etymology.*—The species is named after the type locality, the Santa Rosa Plateau, Riverside Co., California.

*Male.*—Length, 10.1 mm; to telson, 9.0 mm. Habitus (Fig. 2). Lengths of males examined 6.4–10.2 mm. Antenna 2 in form of claspers without frontal process. Distal segment of antenna 2 slender, slightly curved, with row of transverse ridges on inner surface (Fig. 6a, f, h). Tip of segment slightly inflated and bent medially (Fig. 6a, g). Basal portion of row slightly sinuous, contiguous to external edge on distal half of segment (Fig. 10h), not reaching tip. Basal segment of antenna 2 stout with dorsomedially projecting basomedial outgrowth (Figs. 3A, 5F, 6a). Outgrowth with slender, laterally curving tip and spinose plateau on

inner face (Figs. 3B, C, 6a, 7a, f). Spines on plateau smooth and slightly recurved (Fig. 7a, f). Maxilla 2 of common type with single stiff seta on tip and 2–3 soft setae toward base (Cannon & Leak 1933, Linder 1941). Preepipodites of thoracic appendages serrated (Fig. 3E). Endopodite rounded with small spines at the base of setulose setae (Fig. 3D). Penes rectilinear, parallel. Basal part non-retractile, square in cross section, reaching end of third abdominal segment, with slightly curved medially-directed spur ornamented with 3–5 curved spines on inner side (Figs. 3F, 8a, c). Eversible tip of penes with smoothly tapered spine (Fig. 8b). Abdomen with dorsal and ventral setae 60–70 mm long (Fig. 8g, h). Cercopods with fine setae on surface and setulated setae along edges (Fig. 8e, f).

*Female.*—Length 11.1 mm, 10.0 mm to telson, ovigerous. Lengths of females examined 7.2–11.3 mm. Antenna 2 with straight horn-like process originating from inner side of basal segment (Fig. 4A, B). Process with thick base, denticulate on distal half (Fig. 4B). Anterior surface of basal segment hirsute, bearing irregular row of setae at base of the inner process (Fig. 4A, B). Distal segment of antenna 2 small, tapering to point. Brood pouch globular, 1.2 times wider than long, extending to abdominal segment 3. Pore opens subdistally and ventrally (Fig. 4C, D). Resting eggs (=cysts) spherical, with numerous short, tulip-shaped spines (Figs. 9a–i, 10a, c); diameter 230–283  $\mu\text{m}$ , mean diameter,  $260.7 \pm 13.8 \mu\text{m}$ ,

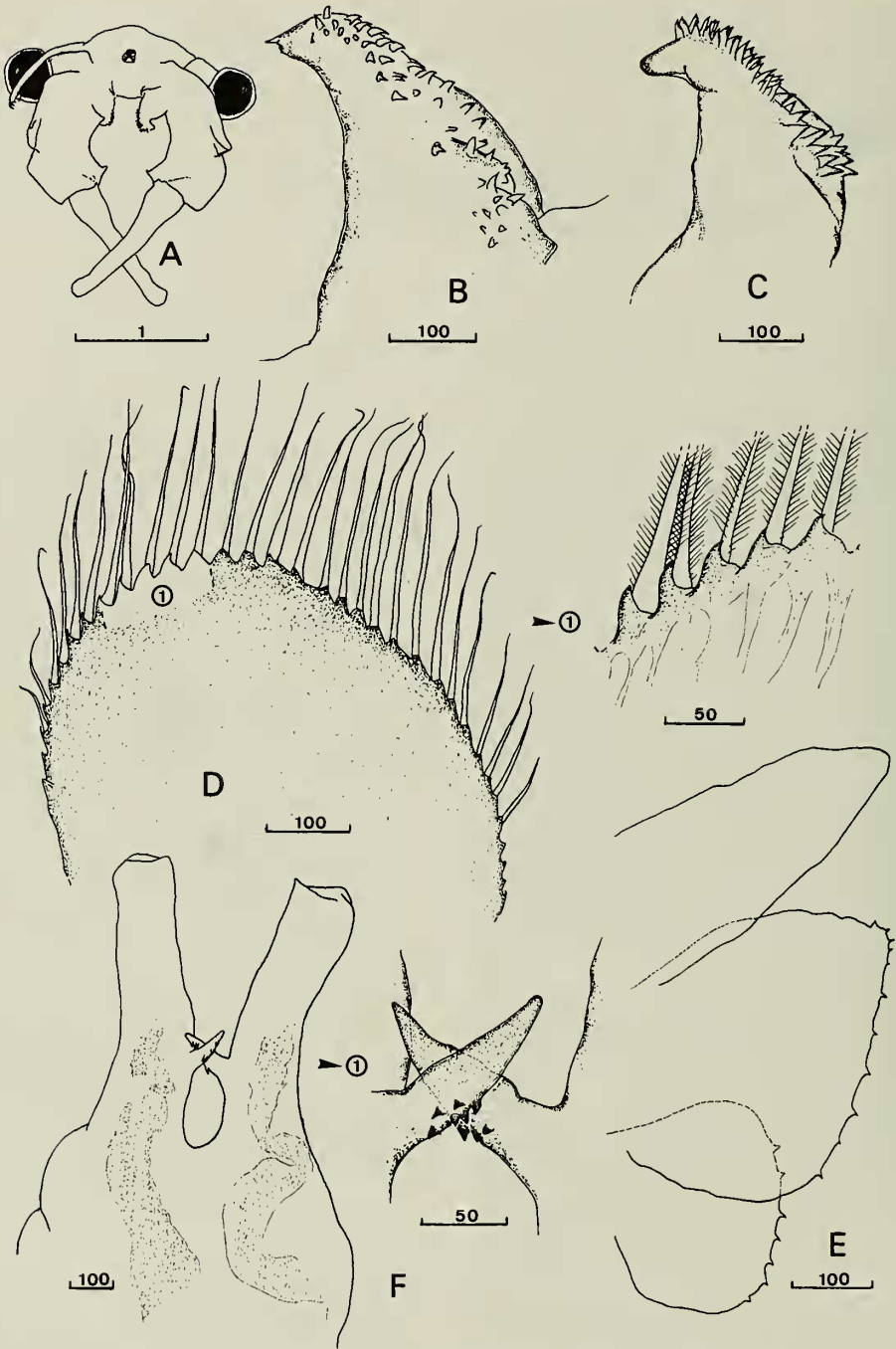


Fig. 3. *Lindieriella santarosae*, n. sp. male: (A) head frontal view; (B) & (C) detail of the basomedial outgrowth; (D) shape of the endopodite of the appendage 7 with an enlarged detail; (E) shape of the preepipodites of the appendage 7; (F) penes in ventral view, tip not everted, with detail of the spurs of the basal nonretractile part (scales in  $\mu\text{m}$ , except for (A) in mm).

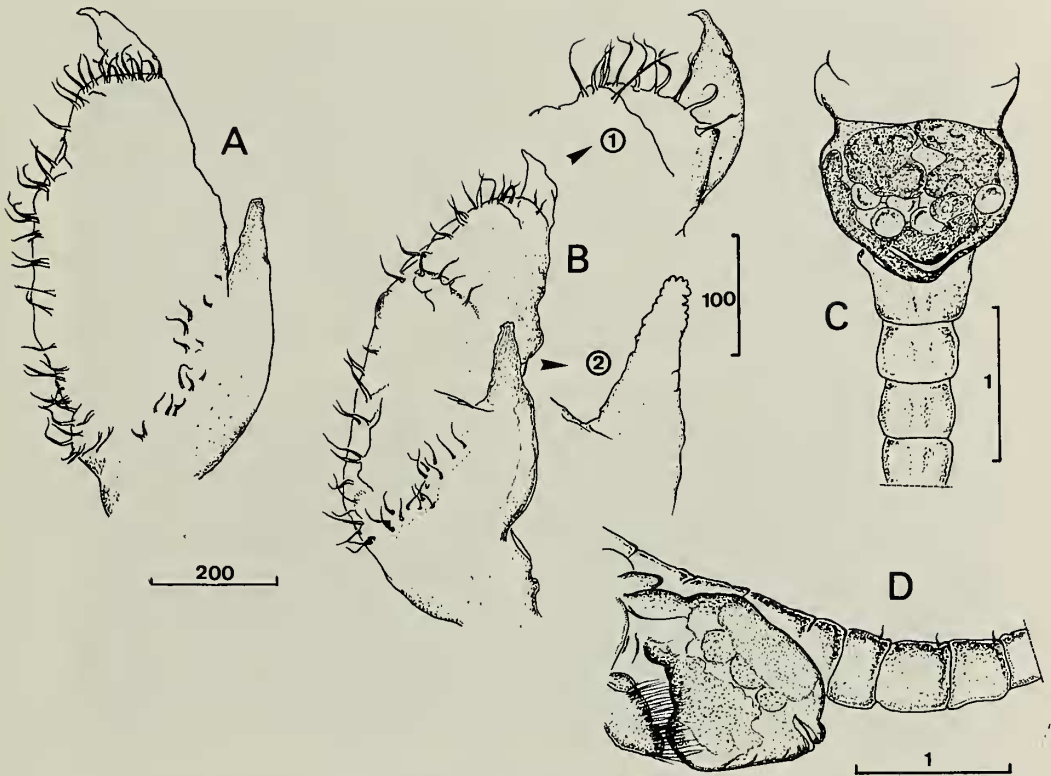


Fig. 4. *Linderiella santarosae*, n. sp. female: (A) & (B) second antenna dorsal view; (C) brood pouch ventral view; (D) brood pouch left lateral view (scales (A) & (B) in mm & (C) (D) in  $\mu\text{m}$ ).

$n = 35$  from three mature females. Spines, 18–23  $\mu\text{m}$  long, with flat tops, 5–16  $\mu\text{m}$  wide (Fig. 9d–i). Most tops open with no pore visible at base of spines. Irregularly, spines fused at bases in twos or threes, making short walls not reaching more than half of total length of spine (Fig. 9a, b). Spinose outer layer surrounding spongy inner layer (Fig. 10d). One of largest mature females (8.2 mm) with 14 eggs in brood pouch.

Females larger than males through same cohort as previously observed for other *Linderiella* species (Dodds 1923, Heath 1924, Thiéry 1986a, Thiéry & Champeau 1988). Living fairy shrimps white, sometimes pale green or blue, quite translucent, with dark red eyes and reddish orange cercopods. Brood pouch of mature female with white shell glands and gold yellow to dark bronze resting eggs.

*Remarks.*—The five species in the genus *Linderiella* are distinguished from one another by only minor morphological differences (Thiéry & Champeau 1988). The undescribed Spanish *Linderiella* was initially identified as *L. occidentalis* (Alonso 1985) and *Linderiella santarosae* was as well in a recent survey of Californian anostracans (Eng et al. 1990). The form of the male antenna 2 and the resting egg are the two most reliable characters for distinguishing *L. santarosae* and *L. occidentalis* (Figs. 5–10), but minor differences are also found in the form of the medial spur on the penis (Fig. 8a–d). The row of transverse ridges on the distal segment of the male antenna 2 of *L. occidentalis* is more sinuous and the tip of the segment is neither sharply bent nor slightly inflated (Figs. 6 & 10h, i). The paired basomedial outgrowths on the basal segment

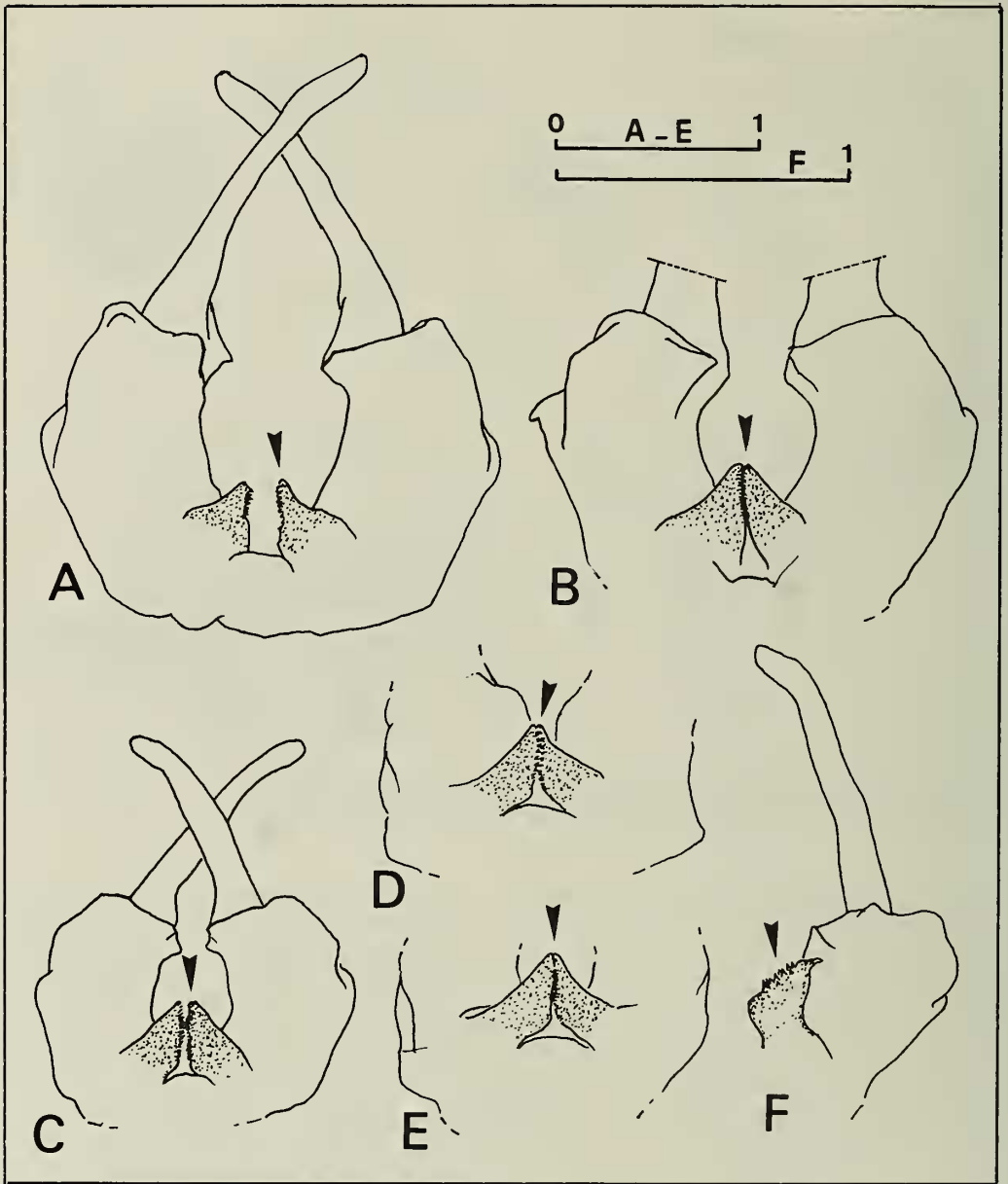


Fig. 5. Comparison of basomedial outgrowth of basal segment of male second antenna between *Lindieriella santarosae*, n. sp. and different populations of *Lindieriella occidentalis* (Dodds): *L. occidentalis*, (a) Tim Bell Rd.; (b) Olsen Rd.; (c) Lagunita Palo Alto; (d) Prairie City OHV; (e) DB. 430; *Lindieriella santarosae*, n. sp.; (f) Santa Rosa Plateau, type locality (scale in mm).

of the male antennae 2 of *L. occidentalis* are similar in form to those of *L. santarosae*, but lack the slender, outward curving tips (Figs. 5, 6a-c, & 7). The resting eggs of *L. occidentalis* have acute spines instead of

short, tulip-shaped (less than 2% of the spines of *L. occidentalis* eggs have a flat top) and the spines are longer in *L. occidentalis* (27–33  $\mu\text{m}$ ) than in *L. santarosae* (18–23  $\mu\text{m}$ ).

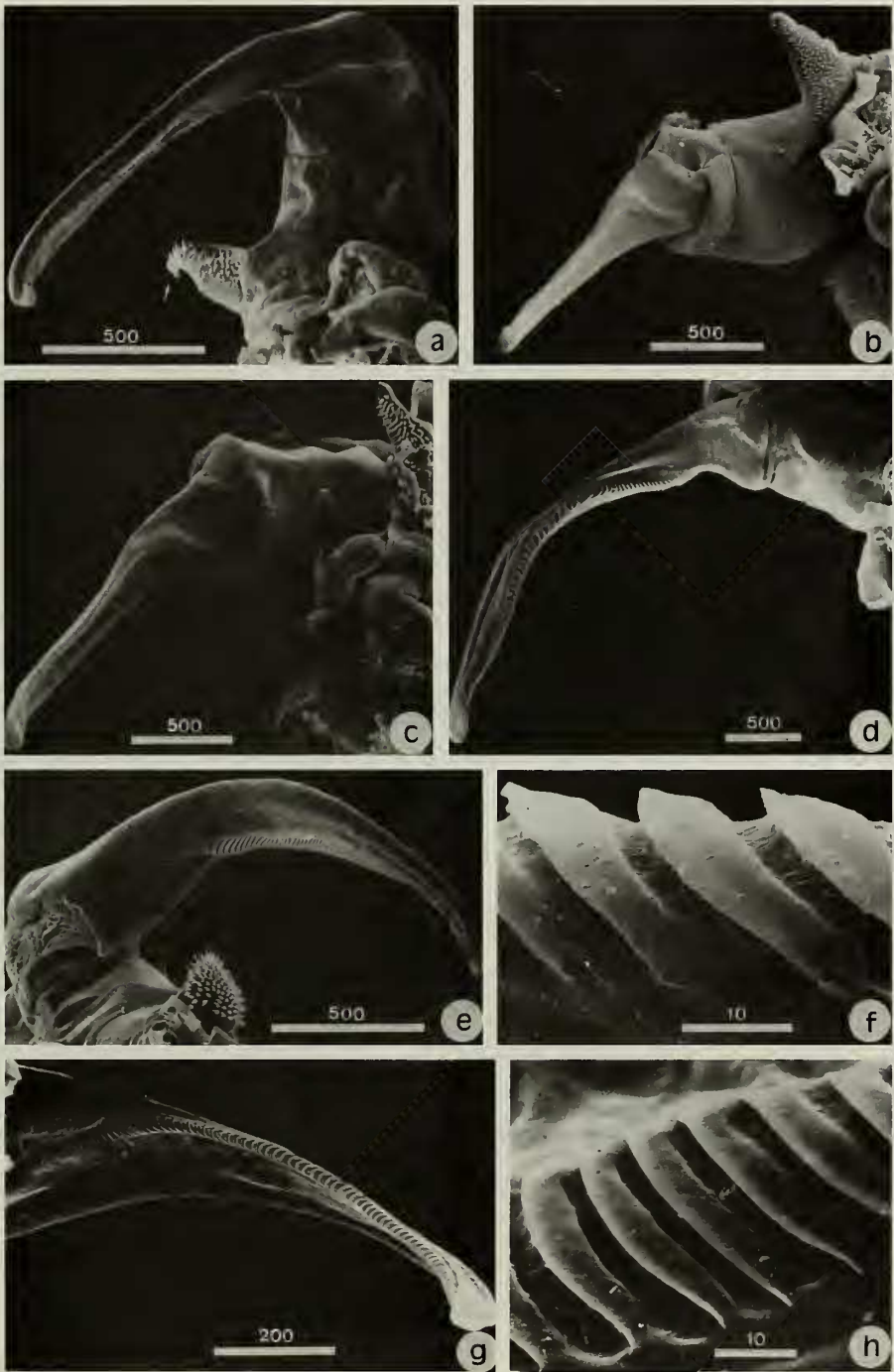


Fig. 6. SEM-micrographs in male second antenna. (a) *L. santarosae*, n. sp., lateral view; (b) inner view of *L. occidentalis* (DB. 430); (c) inner view of *L. occidentalis* (Prairie City); (d) inner view of *L. africana* (Daya Azigza, 6 March 1985, Middle Atlas Morocco); (e) inner view of *L. massaliensis* (pond of St. Maximin, 7 February 1988, France); (f) *L. santarosae*, n. sp., detail of row of transverse ridges, medial part of second segment, lateral view; (g) *L. santarosae*, n. sp., inner view of second segment; (h) *L. santarosae*, n. sp., detail of row of transverse ridges, apical view (scales in  $\mu\text{m}$ ).

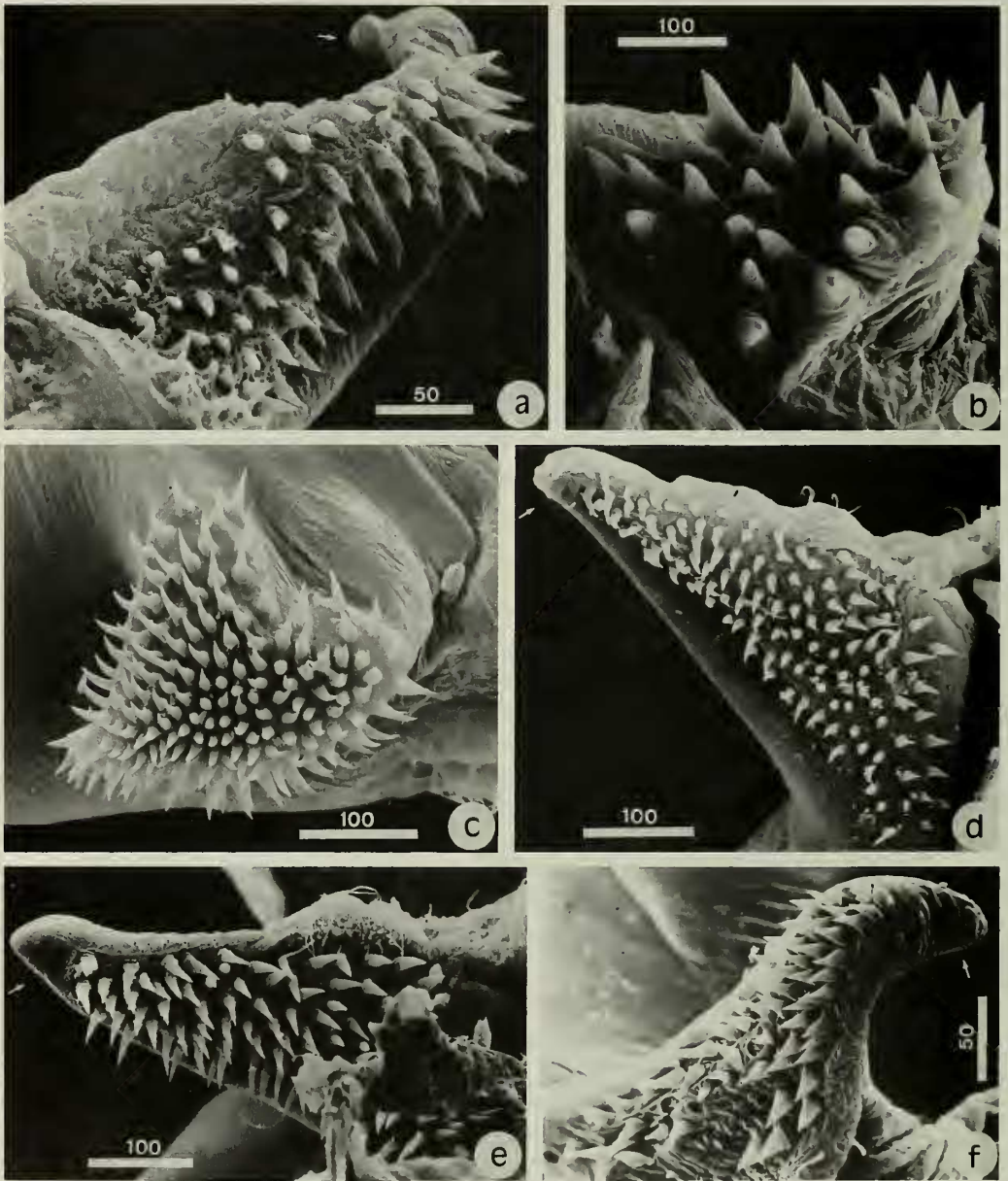


Fig. 7. SEM-micrographs of basomedial outgrowth on inner side of second antennae of males (inner views). (a) *L. santarosae*, n. sp.; (b) *L. africana*; (c) *L. massaliensis*; (d) *L. occidentalis* (DB. 430); (e) *L. occidentalis* (Prairie City); (f) *L. santarosae*, n. sp. (scales in  $\mu\text{m}$ ). Arrows on (a), (d), (e), (f) indicate the straight or curved tip of the basomedial outgrowth.

*Linderiella africana* and *L. massaliensis* (the Spanish *Linderiella* is still undescribed) also differ from *L. santarosae* in the form of the basomedial outgrowth on antenna 2

of the male (Fig. 7) and the spines of the resting eggs (Mura & Thiéry 1986, Thiéry & Champeau 1988). The resting eggs of the Spanish *Linderiella* resemble those of *L.*



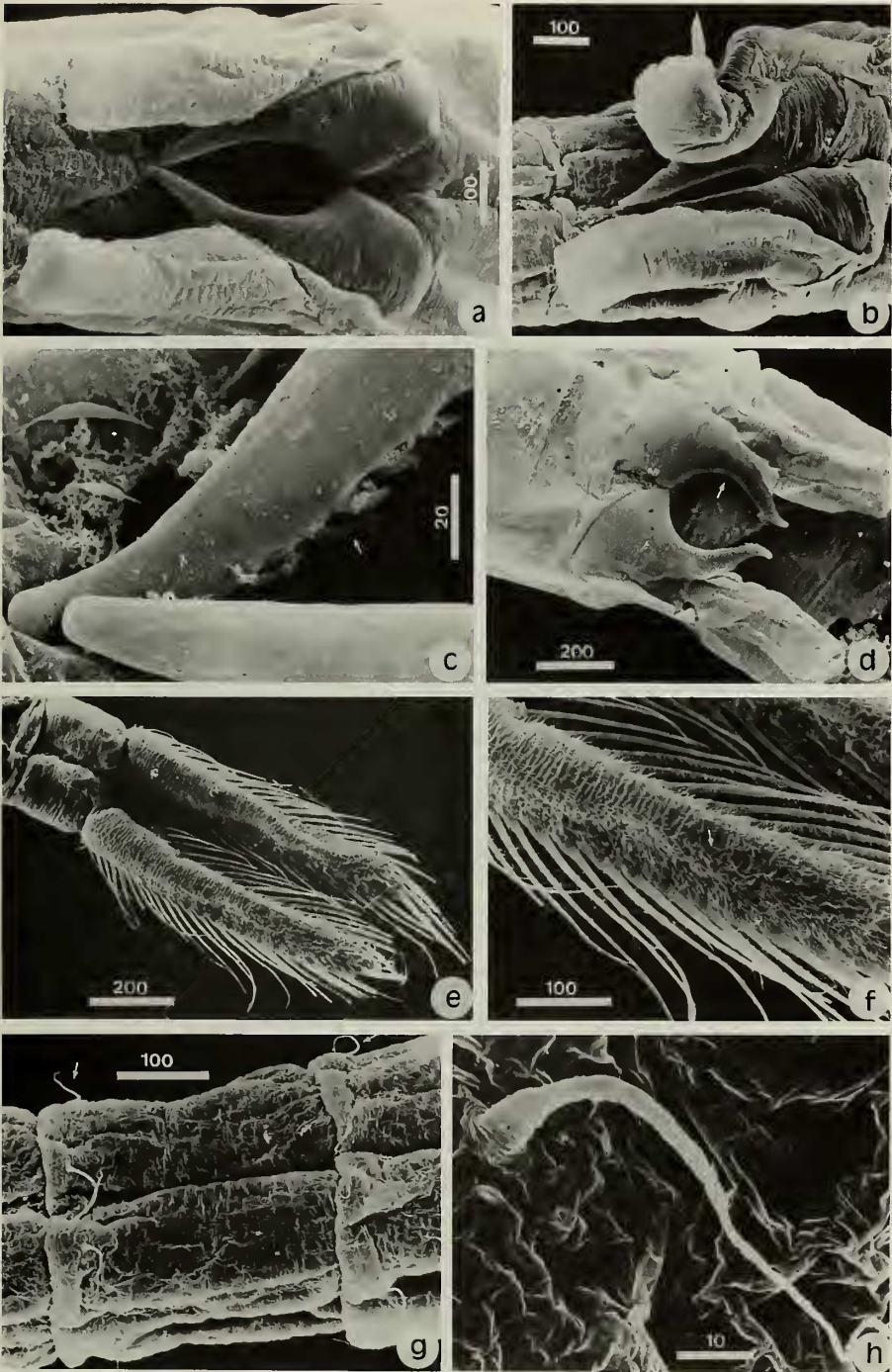


Fig. 8. SEM-micrographs of genital and abdominal segments of males. *Linderiella santarosae*, n. sp. (a-c) & (e-h); (a) ventral view of genital segments of abdomen, nonretractile structures and invaginate penes; (b) idem, with devaginate penes; (c) detail of nonretractile structure, with teeth on inner side (arrow); *Linderiella occidentalis* (DB. 430): (d) ventral view of genital segments of abdomen, with nonretractile parts and invaginate penes (arrow indicates curved inner edge); *Linderiella santarosae*, n. sp.; (e) ventral view of telson and cercopods; (f) detail of cercopods with hirsute surface (arrow); (g) ventral view of abdomen with setae (arrows); (h) detail of an abdominal seta (scales in  $\mu\text{m}$ ).

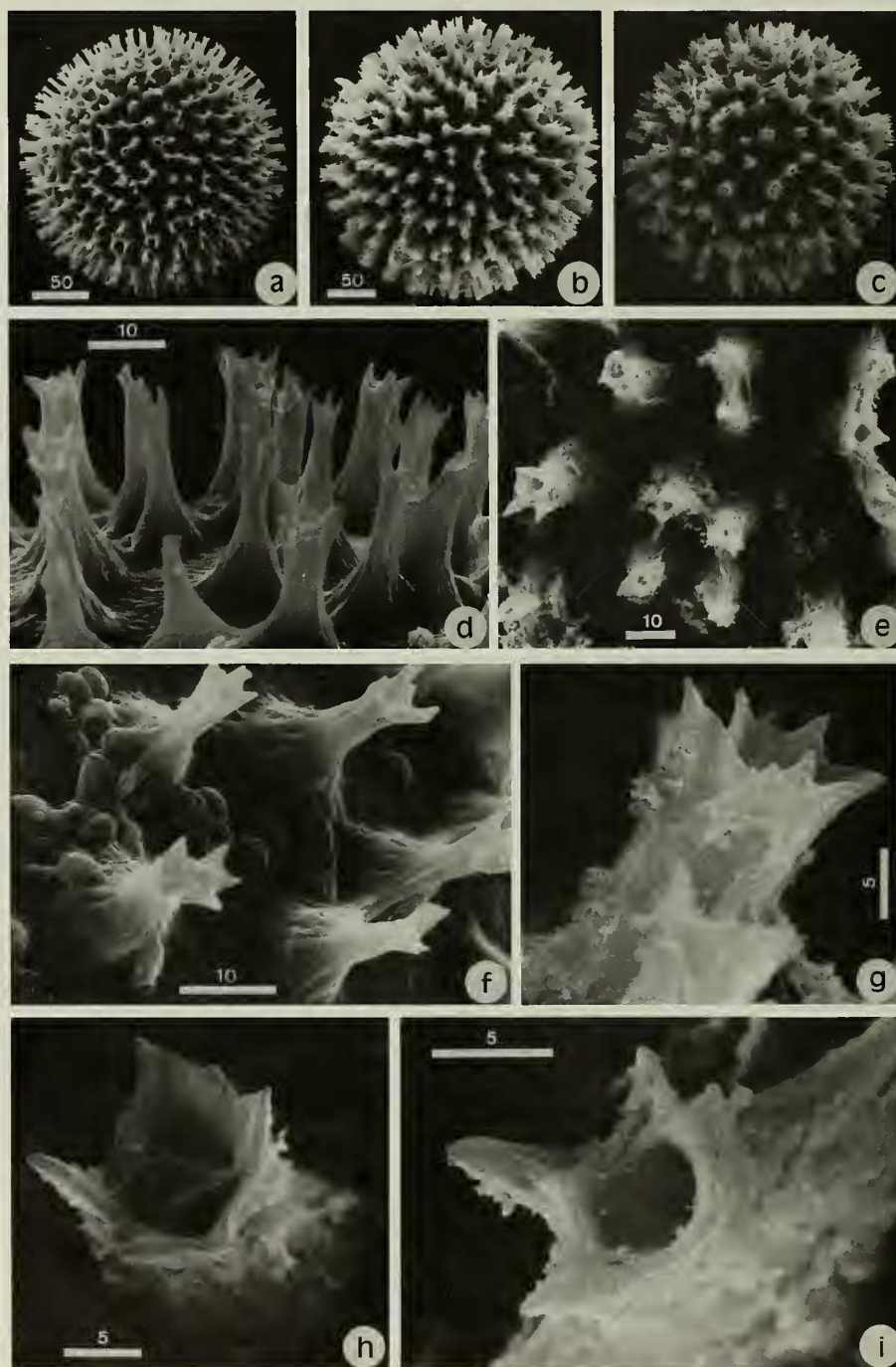


Fig. 9. *Lindieriella santarosae*, n. sp. SEM-micrographs of resting eggs, (a) egg from single female, collected 1 January 1989, (b) & (c) eggs from two different females, collected 1 January 1988; (d) detail of spines, lateral view; (e) detail of spines, apical view; (f) idem, lateral view; (g) detail of a characteristic flat tip, lateral view; (h) detail of a flat tip in apical view; (i) idem, with opened spine (scales in  $\mu\text{m}$ ).

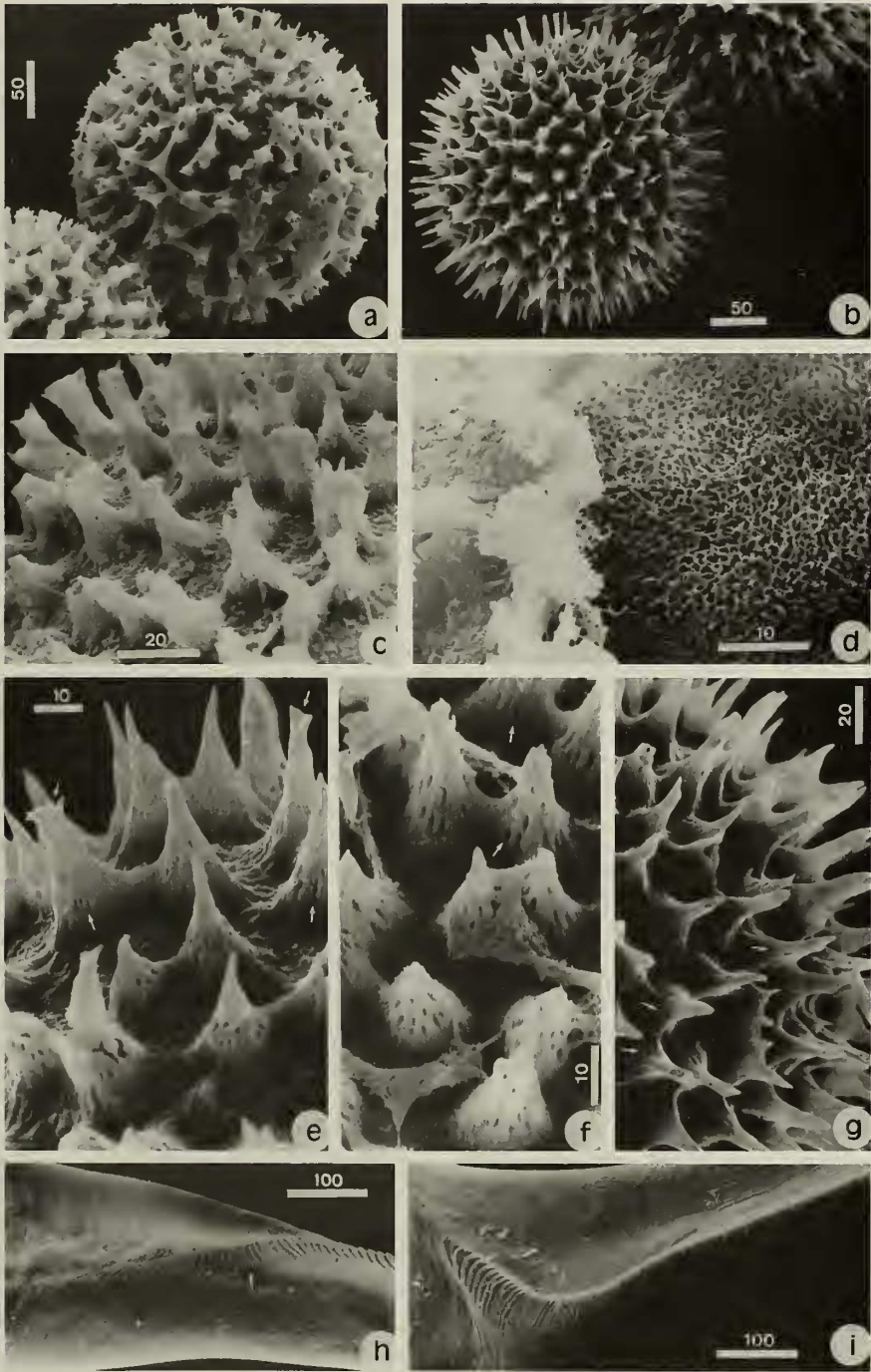


Fig. 10. *Linderiella santarosae*, n. sp. (a), (c), (d), (h) and *L. occidentalis* (b) & (e)—Lagunita, Palo Alto, (f)—Prairie City OHV, (g)—DB. 430; (a) whole egg entangled with mucus; (b) whole egg, with some broken spines (arrows)—(a) & (b) same scale; (c) lateral view of flat top spines; (d) detail of spongy inner layer of egg; (e–g), three detail of acute spines of *L. occidentalis* eggs, with some pores at their bases (arrows indicate pores and some flat top spines); (h) inner view of basal part of second antenna of male (*L. santarosae*, n. sp.) note—slightly sinuous line of rows (arrow); (i) idem, *L. occidentalis*, note the sinuous line more marked (arrow) (scales in  $\mu\text{m}$ ).

Table 1.—Allele frequencies for populations of *Linderiella santarosae*, new species (1 = Mesa de Burro). *Linderiella occidentalis* (2 = Fields Rd., 3 = Tim Bell Rd., 4 = Lagunita), and *Eubranchipus vernalis* (5).

Locus		Population				
		1 (14)	2 (14)	3 (6)	4 (10)	5 (7)
PEP-C	a	0.143	0.000	0.000	0.100	0.000
	b	0.857	1.000	1.000	0.900	1.000
PGI	a	0.000	0.000	0.000	0.100	0.000
	b	1.000	1.000	0.833	0.900	0.000
	c	0.000	0.000	0.167	0.000	1.000
PGM	a	1.000	0.000	0.000	0.000	0.571
	b	0.000	0.000	0.167	0.500	0.429
	c	0.000	1.000	0.833	0.500	0.000
G6PD	a	0.000	0.000	0.000	0.000	0.500
	b	0.000	0.000	0.000	0.000	0.500
	c	0.000	0.000	0.333	0.100	0.000
	d	1.000	1.000	0.667	0.900	0.000
PEP-D	a	0.000	0.071	0.333	0.100	0.000
	b	0.000	0.857	0.667	0.900	0.000
	c	0.000	0.071	0.000	0.000	0.000
	d	1.000	0.000	0.000	0.000	0.000
	e	0.000	0.000	0.000	0.000	0.571
	f	0.000	0.000	0.000	0.000	0.429
ME	a	0.000	0.000	0.000	0.000	0.786
	b	0.000	0.000	0.000	0.000	0.214
	c	1.000	0.429	0.500	0.100	0.000
	d	0.000	0.571	0.500	0.900	0.000
IDH	a	0.000	0.000	0.000	0.100	1.000
	b	1.000	1.000	1.000	0.800	0.000
	c	0.000	0.000	0.000	0.100	0.000
AAT	a	0.000	0.000	0.000	0.000	0.929
	b	1.000	1.000	1.000	1.000	0.071

*santarosae*; this undescribed species also has tulip-shaped spines (Alonso & Alcaraz 1984, Thiéry & Champeau 1988). These differences in resting egg morphology confirm previous studies on the taxonomic value of resting egg ornamentation as a tool for identification of most anostracans (see review in Thiéry & Gasc, 1991, and Mura 1991, 1992a, 1992b).

A preliminary electrophoretic survey potentially provides two additional characters for distinguishing between *L. santarosae* and *L. occidentalis*. Although sample sizes are small (14 *L. santarosae* & 30 *L. occidentalis*), two loci (PEP-D & PGM) show fixed

allelic differences (Table 1). Additional sampling may show these allelic differences to be incompletely fixed, but its unlikely to substantially alter the large genetic distances between the two species. The average D within *Linderiella occidentalis* (3 populations) is 0.054 and between *L. occidentalis* and *L. santarosae* is 0.378 (Fig. 11). These genetic differences are similar to those found between closely related species in the anostracan genus *Branchinecta* (Fugate 1992). For example, *Branchinecta lynchi* and *Branchinecta sandiegonensis* Fugate, 1993 have ranges similar to *L. occidentalis* and *L. santarosae*, respectively (Eng et al. 1990, Fugate 1992, 1993). The average D within *B. lynchi* is 0.154 (9 populations) and between *B. lynchi* and *B. sandiegonensis* (3 populations) is 0.477. A limitation in the electrophoretic analysis arises due to the limited range of *L. santarosae*; the close proximity of the pools on the plateau (<5 km) allows water birds to freely move resting eggs from pool to pool and makes the entire range of the species effectively one population.

*Distribution and habitat.*—*Linderiella santarosae* is currently known only from vernal pools on the Santa Rosa Plateau Reserve, Riverside Co., California. The Santa Rosa Plateau is approximately 300 km southeast of the nearest known populations of *Linderiella* in southern California (Cachuma Canyon, Santa Barbara Co., 34°42'N, 119°54'W, personal collection of Clyde Eriksen, A2-25; Sulfur Mountain, Ventura Co., 34°26'N, 119°06'W, personal collection of Denton Belk DB. 693). These two populations have not been studied electrophoretically, but morphologically appear to be *Linderiella occidentalis*. Another pool, one mile northwest of Olema, Marin Co. and across the road from the Visitors Center at Point Reyes National Seashore, 38°03'N/122°48'W (coll. Gary M. Fellers, collection DB. 878), is reported to have individuals that "look like *L. occidentalis*, but have eggs with some short flat-topped spines" (D. Belk,

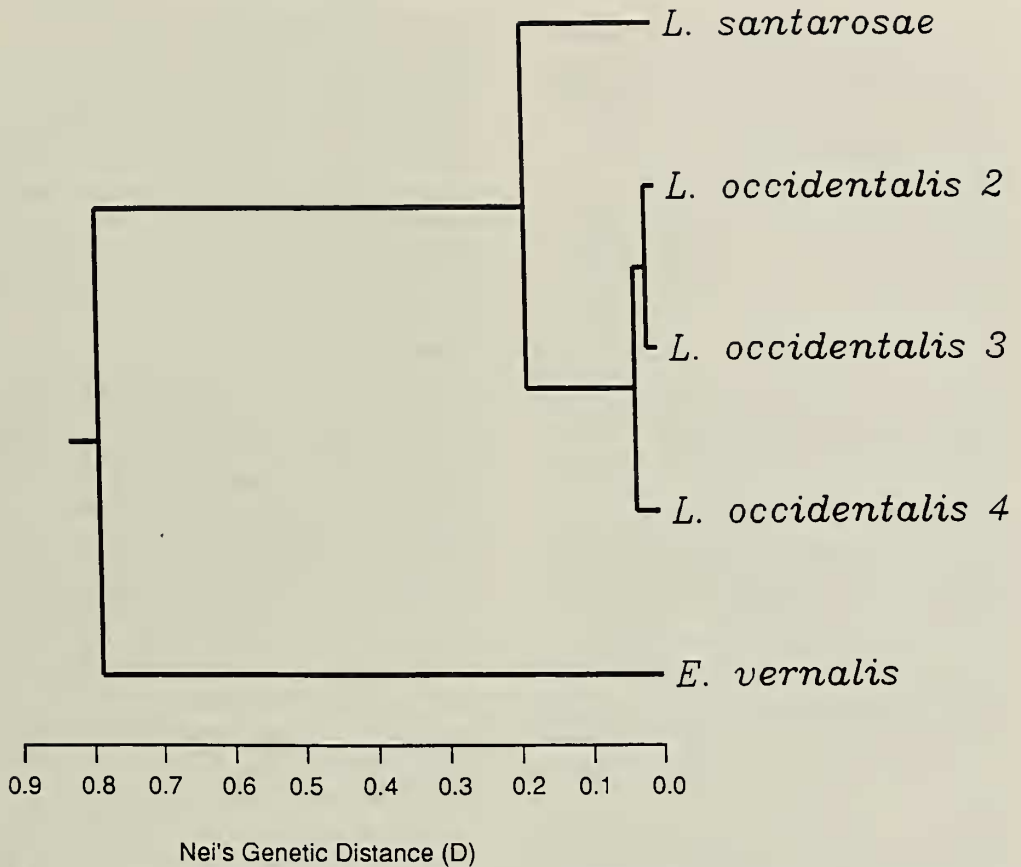


Fig. 11. UPGMA tree of Nei's pairwise genetic distances between populations of *Linderiella occidentalis* and *L. santarosae*. *Linderiella santarosae* 1—Mesa de Burro, *L. occidentalis* 2—Fields Rd., 3—Tim Bell Rd., 4—Lagunita, *Eubranchipus vernalis* 5—Connecticut Valley Biological Supply.

in litt.). We have not seen these individuals, but it would appear unlikely that these are individuals of *L. santarosae*.

The Santa Rosa Plateau Reserve is an isolated unit of grassland and oak-woodland-chaparral in southeastern Riverside Co., California, owned and managed by the Nature Conservancy (Lathrop & Thorne 1968, 1978). Two large (~3 km<sup>2</sup>), flat-topped mesas of volcanic origin are prominent features of the reserve and contain thirteen vernal pools ranging in size from 25 m<sup>2</sup> to over 100,000 m<sup>2</sup>. The mesas are capped by olivine basalt lavas that have weathered to form soils of the Murrieta series. The average elevation of the plateau is 610 m (Lathrop & Thorne 1976a, 1976b, 1983).

Collie & Lathrop (1976) report that pools on the Santa Rosa Plateau normally fill after winter rains (November to April) totaling 30–40 cm. The physico-chemical features of the 13 vernal pools are similar to those of pools containing *L. occidentalis* in other parts of the state (Eng et al. 1990); the conductivity of the water is low (147–189  $\mu\text{mhos cm}^{-1}$  in February to 500–1050 in June), the pH is near 7.0 and water temperatures are usually below 20°C when *L. santarosae* is present (Collie & Lathrop 1976). *Linderiella occidentalis* is also commonly found at temperatures below 20°C and higher temperatures may be limiting to adults (Lanway 1974, Patton 1984, Eng et al. 1990).

The flora of the reserve was listed by Munz

& Keck (1959) and later was characterized in a series of papers by Lathrop (1976), Lathrop & Thorne (1968, 1976a, b, 1978, 1983) and Thorne & Lathrop (1969, 1970). Kopecko & Lathrop (1975) quantified the vegetation in and around the vernal pools on the reserve and reported the following genera and species, also common in pools containing *Lindieriella* from France, Spain and Morocco: *Isoetes*, *Eleocharis*, *Callitriche*, *Juncus*, *Marsilea* and *Ranunculus aquatilis* (Maire 1924, Barbero et al. 1982, Alonso 1985, Thiéry 1987). These genera have been labeled "typical" vernal pool plants in California (Jain 1976).

The fauna of vernal pools on the Santa Rosa Plateau is poorly characterized (Pequegnat 1951), but the branchiopod diversity is much lower than that found associated with the other four *Lindieriella* species (Alonso 1985, Thiéry 1986a, Thiéry & Champeau 1988). The other four species are often found in pools containing notostracans and conchostracans, but neither are present in pools on the plateau. Two amphibians are known to breed in the pools (*Bufo* sp. and *Hyla* sp.), and the following invertebrates are also present after winter rains: *Branchinecta lynchi* (Anostraca), *Moina* sp. (Cladocera), calanoid copepods, Ostracoda, Rotifera and Platyhelminthes.

### Discussion

The modern disjunct distribution of the genus *Lindieriella* has been the subject of some speculation (Belk 1984, Thiéry 1986a, 1986b; Thiéry & Champeau 1988, Banarescu 1990). These authors, using indirect evidence from a variety of sources, have attributed the disjunction to a vicariance event (sensu Bernardi 1986, Wiley 1988) involving the fragmentation of an ancestral taxon distributed across Laurasia. A number of other animal and plant taxa with similar ecologies have either modern or fossil distributions across the Holarctic (e.g., Raven 1971, DiCasteri & Mooney 1973, Banarescu 1990). The limited fossil records of

branchiopods indicates that modern genera may have been formed before the Cretaceous (Trusheim 1938, Tasch 1969, Trusova 1971, Jell & Duncan 1986). Also, dispersal is passive, limited, and more likely to occur in a north-south rather than an east-west direction (Proctor 1964, Proctor & Malone 1965, Cruden 1966, Proctor et al. 1967, Boileau et al. 1992, Fugate 1992, Saunders et al. 1993).

Although the vicariance hypothesis is consistent with the evidence for both ancientness and limited dispersal, the alternative hypothesis of long-distance dispersal cannot be fully eliminated due to the lack of a fossil record and an inadequate understanding of phylogenetic relationships within the Anostraca. The lack of a fossil record is difficult to surmount, but a phylogeny could be reconstructed using morphological, biochemical or molecular characters. The phylogeny could then be employed to test the coincidence between the history of the species within the genus and the history of the geographic regions in which they are currently found (Brooks 1990, Wiley et al. 1991). Until such a test is performed, the vicariance hypothesis will remain speculative.

### Acknowledgments

We thank C. Sassaman (University of California, Riverside), S. Morey (University of California, Riverside), M. Simovich (University of San Diego, California) and G. Bell (Nature Conservancy) for shrimp or soil, D. Belk (Our Lady of the Lake University, Texas) for loaning samples of *L. occidentalis* (DB. 430, DB. 693) and for comments on sample DB. 878, C. Eriksen (Claremont Colleges, California) for loaning samples A2-25, and C. Grill (University of Montpellier, France) for help with the scanning electron microscopy.

### Literature Cited

- Alonso, M. 1985. A survey of the Spanish Euphylopoda.—*Miscellanea Zoologica* 9:179-208.

- , & M. Alcaraz. 1984. Huevos resistentes de crustáceos euilopodos no cladoceros de la península Ibérica: Observación de la morfología externa mediante técnicas de microscopía electrónica de barrido.—*Oecologica Aquatica* 7:73–78.
- Banarescu, P. 1990. Zoogeography of fresh waters. Vol. 1: General distribution and dispersal of freshwater animals. AULA-Verlag, Wiesbaden, 511 pp.
- Barbero, M., J. Giudicelli, R. Loisel, P. Quezel, & E. Terzian. 1982. Étude des biocénoses des mares et ruisseaux temporaires à éphémérophytes dominants en région méditerranéenne française.—*Bulletin d'Ecologie* 13(4):387–400.
- Belk, D. 1984. Patterns in anostracan distribution. Pp. 168–172 in S. Jain & P. Moyle, eds., *Vernal pools and intermittent streams*. Institute of Ecology Publication No. 28, Davis, California.
- Bernardi, G. 1986. La vicariance, la pseudovicariance et la convergence allopatrique.—*Bulletin d'Ecologie* 17(3):145–154.
- Boileau, M. G., P. D. N. Herbert, & S. S. Schwartz. 1992. Non-equilibrium gene frequency divergence: persistent founder effects in natural populations.—*Journal of Evolutionary Biology* 5:25–39.
- Brooks, D. R. 1990. Parsimony analysis in historical biogeography and coevolution. Methodological and theoretical update.—*Systematic Zoology* 39:14–30.
- Brtek, J. 1964. Eine neue Gattung und Familie der Ordnung Anostraca.—*Annotationes Zoologicae et Botanicae, Bratislava* 7:1–7.
- Cannon, H. G., & F. M. Leak. 1933. On the mouth parts of the Branchiopoda.—*Philosophical Transactions of the Royal Society of London, Series B* 222:340–352.
- Collie, N., & E. W. Lathrop. 1976. Chemical characteristics of the standing water of a vernal pool on the Santa Rosa Plateau, Riverside County, California. Pp. 27–31, in S. Jain, ed., *Vernal pools: their ecology and conservation*. Institute of Ecology, Publication No. 9, Davis, California.
- Cruden, R. W. 1966. Birds as agents of long-distance dispersal for disjunct plant groups of the temperate western hemisphere.—*Evolution* 20:517–532.
- Di Castri, F., & H. A. Mooney, eds. 1973. *Mediterranean type ecosystems: origin and structure*. Springer-Verlag, Berlin.
- Dodds, G. S. 1923. A new species of phyllopod.—*Occasional Papers of the Museum of Zoology, University of Michigan* 141:1–3.
- Eng, L. L., D. Belk, & C. H. Eriksen. 1990. Californian Anostraca: distribution, habitat, and status.—*Journal of Crustacean Biology* 10(2):247–277.
- Felsenstein, J. 1989. PHYLIP—Phylogeny inference package (Version 3.2).—*Cladistics* 5:164–266.
- Fugate, M. 1992. Speciation in the fairy shrimp genus *Branchinecta* (Crustacea: Anostraca) from North America. Unpublished Ph.D. Dissertation, University of California, Riverside, 270 pp.
- . 1993. *Branchinecta sandiegonensis*, a new species of fairy shrimp (Crustacea: Anostraca) from western North America.—*Proceedings of the Biological Society of Washington* 106:296–304.
- Heath, H. 1924. The external development of certain phyllopods.—*Journal of Morphology* 38:453–483.
- Jain, S. 1976. Some biogeographic aspects of plant communities in vernal pools. Pp. 15–21 in S. Jain, ed., *Vernal pools. Their ecology and conservation*. Institute of Ecology Publication No. 9, Davis California.
- Jell, P. A., & P. M. Duncan. 1986. Invertebrates, mainly insects, from the freshwater, Lower Cretaceous, Koonwarra Fossil Bed (Korumburra Group), South Gippsland, Victoria.—*Association of Australasian Palaeontologists, Memoirs* 3:111–205.
- Kopecko, K. J. P., & E. W. Lathrop. 1975. Vegetation zonation in a vernal marsh on the Santa Rosa Plateau of Riverside County, California.—*Aliso* 8(3):281–288.
- Lanway, C. S. 1974. Environmental factors affecting crustacean hatching in five temporary pools. Unpublished M.S. thesis, Department of Biological Sciences, Chico State University, Chico, California, 89 pp.
- Lathrop, E. W. 1976. Vernal pools of the Santa Rosa Plateau, Riverside County, California. Pp. 22–27 in S. Jain, ed., *A symposium, Vernal pools, their ecology and conservation*. Institute of Ecology, Publication No. 9, Davis, California.
- , & R. F. Thorne. 1968. Flora of the Santa Rosa Plateau of the Santa Ana Mountains, California.—*Aliso* 6(4):17–40.
- , & ———. 1976a. The Vernal pools of Mesa de Burro of the Santa Rosa Plateau, Riverside County, California.—*Aliso* 8(4):433–445.
- , & ———. 1976b. Vernal pools of the Santa Rosa Plateau, Riverside County, California.—*Fremontia* 4:9–11 (illustrations also 12–17).
- , & ———. 1978. A flora of the Santa Ana Mountains, California.—*Aliso* 9(2):197–278.
- , & ———. 1983. A flora of the vernal pools on the Santa Rosa Plateau, Riverside County, California.—*Aliso* 10(3):449–469.
- Linder, F. 1941. Contribution to the morphology and the taxonomy of the Branchiopoda Anostraca.—*Zoologiska Bidrag från Uppsala* 20:101–302.
- Maire, R. 1924. Études sur la végétation et la flore du Grand Atlas et du Moyen Atlas marocains.—

- Mémoires de la Société des Sciences Naturelles du Maroc 7:5–200 + 16 pl.
- Munz, P. A., & D. D. Keck. 1959. A California flora. University of California Press, Berkeley, 1681 pp.
- Mura, G. 1991. SEM morphology of resting eggs in the species of the genus *Branchinecta* from North America. — *Journal of Crustacean Biology* 11(3): 432–436.
- . 1992a. Pattern of egg shell morphology in thamocephalids and streptocephalids of the New World (Anostraca). — *Crustaceana* 62(3): 300–311.
- . 1992b. Additional remarks on cyst morphometrics in the anostracans and its significance. Part II: egg morphology. — *Crustaceana* 63(3): 225–246.
- , & A. Thiéry. 1986. Taxonomical significance of scanning electron microscopic morphology of the Euphyllopods' resting eggs from Morocco. Part I. Anostraca. — *Vie et Milieu* 36:125–131.
- Nei, M. 1987. Molecular evolutionary genetics. Columbia University Press, New York, 512 pp.
- Patton, S. E. 1984. The life history patterns and the distribution of two Anostraca. *Lindieriella occidentalis* and *Branchinecta* sp. Unpublished M.A. thesis, California State University, Chico, California, 50 pp.
- Pequegnat, W. E. 1951. The biota of the Santa Ana Mountains. — *Journal of Entomological Zoology* 42:1–84.
- Proctor, V. W. 1964. Viability of crustacean eggs recovered from ducks. — *Ecology* 45(3):656–658.
- , & C. R. Malone. 1965. Further evidence of the passive dispersal of small aquatic organisms via the intestinal tract of birds. — *Ecology* 46: 728–729.
- , ———, & V. L. DeVlaming. 1967. Dispersal of aquatic organisms: viability of disseminules recovered from the intestinal tract of captive Kildeer. — *Ecology* 48(4):672–676.
- Raven, P. H. 1971. The relationships between 'Mediterranean' floras. Pp. 119–134 in P. H. Davis, P. C. Harper, & I. C. Hedge, eds., *Plant life of South-West Asia*. The Botanical Society of Edinburgh, Edinburgh.
- Saunders, J. F., D. Belk, & R. Dufford. 1993. Persistence of *Branchinecta paludosa* (Anostraca) in southern Wyoming with notes on zoogeography. — *Journal of Crustacean Biology* 13(1): 184–189.
- Tasch, P. 1969. Branchiopoda. Pp. 128–191 in R. C. Moore, ed., *Treatise on invertebrate paleontology*, Part R—Arthroda 4, vol. 1. Geological Society of America & University of Kansas Press, Lawrence, Kansas.
- Thiéry, A. 1986a. *Lindieriella africana* n. sp., premier représentant des Lindieriellidae (Branchiopoda, Anostraca) en Afrique du Nord (Maroc). — *Crustaceana* 51(2):155–162.
- . 1986b. Les Crustacés Branchiopodes (Anostraca, Notostraca et Conchostraca) du Maroc occidental I. Inventaire et répartition. — *Bulletin de la Société d'Histoire Naturelle de Toulouse* 122:145–155.
- . 1987. Les Crustacés Branchiopodes Anostraca, Notostraca et Conchostraca des mares temporaires (Dayas) du Maroc occidental. Taxonomie, Biogéographie, Écologie. Unpublished Thesis Doctorat es Science, Université d'Aix-Marseille III, 405 pp.
- , & A. Champeau. 1988. *Lindieriella massaliensis*, new species (Anostraca: Lindieriellidae), a Fairy shrimp from Southeastern France, its ecology and distribution. — *Journal of Crustacean Biology* 8(1):70–78.
- , & C. Gasc. 1991. Resting eggs of Anostraca, Notostraca, and Spinicaudata (Crustacea, Branchiopoda) occurring in France: identification and taxonomical value. — *Hydrobiologia* 212:245–259.
- Thorne, R. F., & E. W. Lathrop. 1969. A vernal marsh on the Santa Rosa Plateau of Riverside County, California. — *Aliso* 7(1):85–95.
- , & ———. 1970. *Pilularia americana* on the Santa Rosa Plateau, Riverside County, California. — *Aliso* 7:149–155.
- Trusheim, F. 1938. Triopsiden (Crustacea, Phyllopoda) aus dem Keuper Frankens. — *Palaeontologische Zeitschrift* 19:198–216.
- Trusova, Y. K. 1971. O pervoy nakhodkye v mazozye predstavitoley otryada Anostraca. (First discovery of members of the order Anostraca (Crustacea) in the Mesozoic.). — *Paleontological Journal* 4:68–73.
- Verill, A. E. 1869. Descriptions of some new American phyllopod Crustacea. — *American Journal of Science* 48:244–254.
- Wiley, E. O. 1988. Vicariance biogeography. — *Annual Review of Ecology and Systematics* 19:513–542.
- , D. Siegel-Causey, D. R. Brooks, & V. A. Funk. 1991. The compleat cladist: a primer of phylogenetic procedures. — *The University of Kansas, Museum of Natural History, Special Publication No. 19*, 158 pp.

(AT) Department of Animal Biology-Hydrobiology, Faculty of Sciences, 33 rue Louis Pasteur, University of Avignon, 84000 Avignon, France; (MF) Department of Biology, University of California, Riverside, California 92521, U.S.A.